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# Network-based analysis reveals differences in plant assembly between the native and the invaded ranges

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## Abstract

Associated with the introduction of alien species in a new area, interactions with other native species within the recipient community occur, reshaping the original community and resulting in a unique assemblage. Yet, the differences in community assemblage between native and invaded ranges remain unclear. Mediterranean grasslands provide an excellent scenario to study community assembly following transcontinental naturalisation of plant species. Here, we compared the community resemblance of plant communities in Mediterranean grasslands from both the native (Spain) and invaded (Chile) ranges. We used a novel approach, based on network analysis applied to co-occurrence analysis in plant communities, allowing us to study the co-existence of native and alien species in central Chile. This useful methodology is presented as a step forward in invasion ecology studies and conservation strategies. We found that community structure differed between the native and the invaded range, with alien species displaying a higher number of connections and, therefore, acting as keystones to sustain the structure within the invaded community. Alien species acting like keystones within the Chilean grassland communities might exacerbate the threat posed by biological invasions for the native biodiversity assets. Controlling the spread of the alien species identified here as keystones should help managing potential invasion in surrounding areas. Network analyses is a free, easy-to-implement and straightforward visual tool that can be widely used to reveal shifts in native communities and elucidate the role of multiple invaders into communities.

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**Keywords**
Alien species, Chile, community assembly, co-occurrence, invasion ecology, Mediterranean grasslands, network analysis, Spain, transcontinental naturalisation

## Introduction

Associated with anthropogenic activities, human beings have drastically increased the flow of plant species amongst distant regions worldwide, overcoming major biogeographical barriers and enhancing invasion events (Valladares et al. 2019). When species arrive in a new area, they undergo different adaptative processes related to the degree of disturbance, resource availability and species interactions (Silvertown 2004; Knapp and Kühn 2012). When these species, considered *alien*, become self-maintaining for long-lasting populations without human intervention, they are considered *naturalised* (Richardson et al. 2000; Pyšek et al. 2004). There are several hypotheses proposed to explain this naturalisation process which can be summarised in three non-exclusive main groups: propagule pressure, abiotic filters and biotic interactions (Catford et al. 2009). The combination and characteristics of these three hypotheses drive the naturalisation process to occur (Hastings 1996; Wilson et al. 2007). Understanding how naturalisation affects plant diversity in the invaded community has been a major issue for ecologists (Sutherland et al. 2013), as it entails changes in its assembly and dynamics (Heger and Trepl 2003; Cramer et al. 2008).

Community assembly is a deterministic phenomenon in which a regional pool of species interacts to form local communities that are ultimately influenced by stochastic events, migration, dispersal, abiotic factors, biotic interactions and evolutionary and biogeographic processes (Ricklefs 1987; HilleRisLambers et al. 2012). Along the assembly process, the species either segregate because of competitive processes, aggregate due to facilitation and tolerance or are randomly distributed (Ricklefs 1987; Götzenberger et al. 2012), therefore displaying a particular spatial structure within the community (Ulrich 2004). For alien plant species, comparing assembly patterns between the native and the invaded ranges, can provide valuable information not only about the ecological factors underlying the community assembly (Hortal et al. 2012), but also about unravelling what determines invasion success (Figueroa et al. 2004). Plenty of literature compares abundance between native and invaded ranges and most of them agree that, when both ranges share a vast number of species and environmental conditions, the abundance of alien species is expected to be similar in both, perchance being an indicator of invasion success (Firn et al. 2011; Parker et al. 2013; Colautti et al. 2014; Pearson et al. 2018). Furthermore, some studies have already compared the community composition between Mediterranean grasslands in the native and invaded ranges (for example, Leiva et al. 1997; Martín-Forés et al. 2014), but there are very few that compare their assembly (de Miguel et al. 2016; Galán Diaz et al. 2020).

Network analysis is a novel approach that has become a potent tool to study microbiology communities (Barberán et al. 2012; Chun et al. 2020) and food webs (Bauer et al. 2010). Network analysis can also be applied to study community assemblage (Girvan and Newman 2002; Proulx et al. 2005; Fortunato 2010; Calatayud et al. 2020); however, as far as we are aware, it has yet been unused to compare co-occurrence patterns in plant communities. Network analysis, applied to patterns of flora co-occurrence, can unravel new insights into interaction networks. This will complement the information on naturalisation processes provided by more traditional analytical methods as richness and diversity indexes (Steele et al. 2011; Williams et al. 2014; Ma et al. 2016). In addition, network analysis, applied to invaded communities, elucidates the role of successful invaders by identifying species acting as keystones in the community structure and assemblage (i.e. those species that fulfil a key role within a community or those involved in a significant number of interactions; Estrada 2007; Bauer et al. 2010; Martín González et al. 2010; Eiler et al. 2012).

The dynamics and stability of complex networks are directly related to their structure, where not all the nodes, in this case corresponding to species, assume the same relevance. When nodes with high importance are subsequently removed, the network structure collapses faster than when random nodes are removed (Albert et al. 2000; Memmott et al. 2004). The importance of a node can be quantified by centrality measures, like "betweenness centrality", which provides information on how the node connects different parts of the network (Freeman 1978; Newman 2003). Thus, the betweenness centrality score applied to plant communities helps identify the contribution of each species to the cohesion of the network (Newman 2003).

The Mediterranean-climate regions constitute an excellent scenario for assessing the questions of plant transcontinental naturalisations, as they share similar climatic conditions, but maintain considerable geographic distance amongst them (Guerin et al. 2014, 2018; Martín-Forés 2017; Casado et al. 2018). Concretely, the grasslands of the Mediterranean Basin and the Chilean Mediterranean Region are ideal candidates to explore how species assemble once they become naturalised. Both ranges have shared an historical-cultural legacy since the Spanish arrival in the 16$^{th}$ century. This resulted in an asymmetry in the direction of introduction of species which occurred mainly from the Mediterranean Basin to central Chile and only occasionally in the opposite direction (Casado et al. 2018). Such introduction of alien species from Spain to Chile took place in a sequential and relatively independent process (Groves and Di Castri 1991; Martín-Forés et al. 2012; Casado et al. 2015; Martín-Forés 2017).

Spatial patterns as a result of the co-existence between native and alien species in central Chile have recently been studied through null models by de Miguel et al. (2016). In this study, the authors conclude Chilean grasslands maintain a similar segregated spatial pattern to the Spanish ones. It seems that, in spite of the relatively recent introduction of alien species in Chile, native and alien species have assembled, establishing associations different from random amongst them. Surprisingly, a longer co-existence time between species in Spanish communities was not reflected in a

different spatial pattern than in Chile. However, there is a knowledge gap regarding the differences in the internal structure (e.g. nodes, "betweenness centrality" score, amongst other parameters) of plant communities between Spain and Chile.

This paper is part of a larger study in which we targeted all the steps of the naturalisation process. We targeted the flows of species introductions amongst the Mediterranean regions (Casado et al. 2018) and the state-of-the-art of the species introductions in the Mediterranean Region of Chile (Martín-Forés et al. 2012). Regarding community assembly, we studied abiotic and biotic factors, filtering the community in both the native and the invaded range (Martín-Forés et al. 2015) and explored co-incident changes that could be driving such naturalisation processes (Casado et al. 2015). We also studied how co-occurrence amongst the species within each community differed in both ranges (de Miguel et al. 2016) and, within the invaded range, how plant communities evolved over time through natural succession (Martín-Forés et al. 2016). Besides, for three alien species, we studied trait differences displayed between both ranges (Martín-Forés et al. 2017, 2018a, b).

In this work, we carried out network-based analysis to compare community structure and species co-occurrence between plant communities in the native and invaded ranges. We hypothesised that the pool of species that co-exist in the native range, once they have naturalised, will become organised similarly within the invaded community. Therefore, here we: i) assess the similarity between the Chilean and Spanish communities by comparing their floristic composition and abundance, as well as how alien species associate with each other and with native species and ii) elucidate how the alien species pool has integrated and assembled with the native flora in the invaded range by applying network analysis.

## Methodology

### Study area

The study area is located in the centre-west of Spain (40°13'N to 37°51'N and from 4°23'W to 7°02'W) and central Chile (32°35'S to 37°00'S and from 70°46'W to 72°35'W) (Fig. 1). Both countries share similar land management and physiognomy, based on grasslands. In Spain, this is a historical anthropogenic landscape that transformed woodlands into pseudo-savannah (Le Houerou 1981; López Sáez et al. 2007) where holm oaks (*Quercus ilex subsp. ballota*) and cork oaks (*Quercus suber*) are accompanied by herbaceous species, usually winter annuals (Joffre et al. 1999; Marañón et al. 2009). Meanwhile, in Chile, the anthropogenic landscape is relatively young, associated with the Spanish arrival in the 16$^{th}$ century (Aronson et al. 1998; Figueroa and Jaksic 2004). As a consequence, the pre-colonisation scrub and forest vegetation (Di Castri et al. 1981) was transformed into a landscape of scattered *Acacia caven* mixed with alien and native annual species (Aronson et al. 1998; del Pozo et al. 2006).

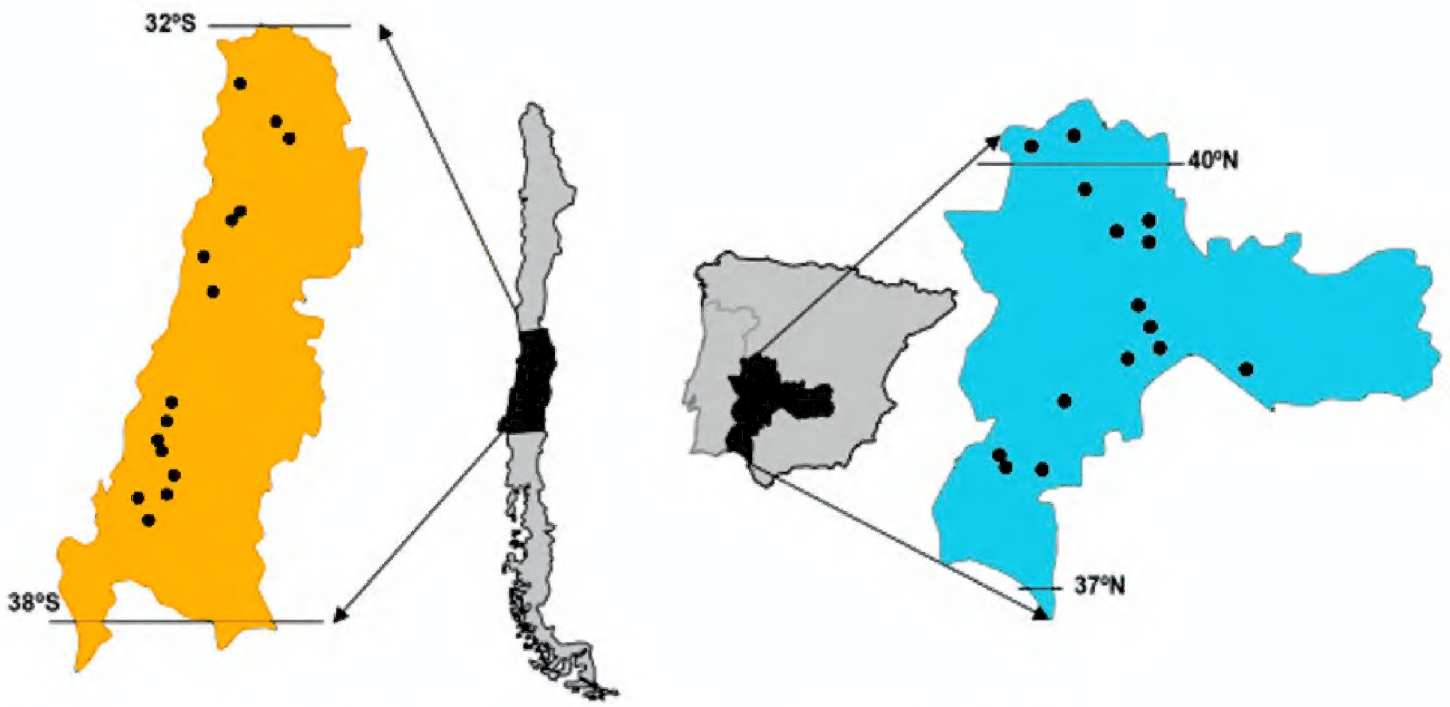


**Figure 1.** Map of the study areas Chile and Spain, sampling sites as points.

The agrarian practices introduced in central Chile involved a significant flow of organisms between Spain and Chile with the implementation of agriculture and grazing practices. This flow has persisted over time, possibly taking place unintentionally associated with human transport (Groves and Di Castri 1991; Ovalle et al. 2015; Martín-Forés 2017; Casado et al. 2018). Due to the history of land use and disturbance of Chile's grasslands, almost half of its vegetation is composed of alien species, with Eurasia and the Mediterranean Basin being the main donors (Casado et al., 2018). The most representative families in the Chilean grasslands (Poaceae, Asteraceae and Fabaceae) are also the most dominant in the Spanish grasslands. Not only qualitatively, but also quantitatively, those systems have similarities: amongst the ten most abundant species in Chilean grasslands, 90% are native Spanish herbaceous species that became naturalised in Chile; similarly, amongst the ten most abundant species of Spanish grasslands, 90% are common with Chile and, therefore, successful colonisers in Chile (Martín-Forés et al. 2012).

Regarding abiotic conditions, both areas have mean annual temperatures ranging from 14.5 °C to 16.9 °C in Chile and from 13.1 °C to 17.0 °C in Spain. The total annual precipitation of the sites ranges from 468 to 1030 mm in Spain and from 303 to 1168 mm in Chile. The summer drought period, characteristic of Mediterranean-climate, is more intense in Chile than in Spain. Both systems have slightly acid soils from igneous or metamorphic rocks (Martín-Forés et al. 2015; de Miguel et al. 2016).

## Data origin

The data utilised in this paper have been obtained in the previous study by Martín-Forés et al. (2015). In that study, vegetation surveys were carried out in both Medi-

terranean-climate regions described above (see study area). In both countries, 15 sites were selected to cover the range of climatic conditions found in Mediterranean-type regions (Fig. 1; see Martín-Forés et al. 2015 for methodological details regarding the climatic gradients considered). The study system in all sites had a similar physiognomy, opened savannah-like woodlands with only a few scattered trees and similar values of woody cover. Land-use was also similar in systems of both countries, mainly extensive grazing by cattle and sheep (Ovalle et al. 2015). Locally, we observed some differences in the livestock load that varied between one to two sheep per hectare in Chile and between one to three sheep per hectare in Spain, possibly related to the greater or lesser seasonal heterogeneity of the herbaceous production potential (Ovalle et al. 1990). In each site, vegetation surveys were carried out in twelve 50 × 50 cm quadrats that were randomly distributed in open areas to avoid tree influence (Marañón et al. 2009; De Miguel et al. 2013). Therefore, 180 quadrats were surveyed for each country in 2011, in which we scored species richness and abundance, estimated as presence within the twelve quadrats within each site. In the analysis, only herbaceous species were considered, as naturalisation success depends on plant life form (Tecco et al. 2010) and around 90% of alien species are herbaceous (Fuentes et al. 2013).

A total of 262 species were identified between both countries (190 species appeared in Spain and 132 appeared in Chile) and classified into four groups: i) *alien species*, those native to Spain that have been naturalised in Chile (111 species); ii) *Spain exclusive species*, which includes native and alien non-Chilean species, which only occur in Spain (91 species); iii) *Chilean native species*, which are native to Chile and do not occur in Spain (55 species); iv) *other species*, those non-included species in the previous groups, which are Chilean native species that occur in Spain and native species to both countries (5 species). We did not include the group *other species* in the analysis, as the aim here was to compare alien species in both ranges. Hence, in this study, we have worked with three sets of species: *alien species*, *Spanish exclusive species* and *Chilean native species*.

## Data analysis

The data obtained during the surveys were organised in two datasets: i) a presence-absence dataset that contained this information for every species in each of the 30 sites (15 sites per country) and ii) a dataset that included abundance information from 0 to 12 quadrants of each specie for all of the 30 sites.

To analyse the community resemblance between Spain (native range) and Chile (invaded range), we made a Non-metric Multidimensional Scaling (nMDS), based on the Bray-Curtis dissimilarity matrix with the abundance data of all species and only with alien species. To compare the species co-occurrence patterns between the native and invaded ranges, we followed the probabilistic model developed by Veech (2013). This model analyses the probability that two species co-occur at a lower or greater frequency than the one observed without relying on randomisations. When two species co-occur at a greater frequency than that expected at random, they are considered to have a positive association.

On the contrary, if this frequency is less than expected at random, they are considered to have a negative association. We analysed the presence-absence data of species for each country. In both ranges, we analysed two subsets of species: i) *all species* (i.e. alien plus exclusive in Spain and alien plus native in Chile) and ii) *alien* species on their own. Notice that, in both ranges, the dataset of *alien* species is the same, but with different species abundances.

For the network analysis, we constructed four networks with the co-occurrence analysis results with *all* the species: one for each range and, within each range, one for each type of association (positive or negative). In network analysis terms, the species are considered *nodes* and the associations are considered *edges*. For each network, different parameters were calculated: density, "assortativity" coefficient and assortativity degree. Density represents the ratio between the number of connections existing in the network and the number of possible connections; it ranges from 0 to 1 and gives information on how interconnected the network is (in ecological theory, it is also known as connectivity). The assortativity coefficient measures the selective linking between nodes and ranges from -1 to +1. Positive assortativity values indicate that nodes of a certain species group connect to other nodes of the same species' group (i.e. alien species, native species or exclusive species), while negative values indicate that nodes tend to connect with nodes of a different species group. The assortativity degree measures whether nodes with a high degree (i.e. level of connection to other nodes) connect to other nodes with a high degree, ranging from -1 to +1. Positive assortativity degree indicates well-connected nodes tend to connect with other well-connected nodes, whereas negative values indicate that well-connected nodes tend to connect to poorly connected nodes, giving information about the robustness of the network. Additionally, we calculated the betweenness score for each species in the network, which is defined by the number of paths through a node and gives information about the importance of the species in the community structure. In this sense, nodes with high values of betweenness connect areas of the network that otherwise would be unconnected, possibly acting as keystones (for more information see Newman 2003; Fortunato 2010; Noldus and Mieghem 2014). In this work, a "betweenness" score above 0.1 was arbitrarily considered as the cut-off point to compare ranges.

We carried out all analysis with R software 3.6 version (R Core Team 2015) using the *vegan* package (Oksanen et al. 2020) for the nMDS, the *cooccur* package (Griffith et al. 2016) for the co-occurrence analysis and the *igraph* package (Csardi and Nepusz 2006) for the network analysis and visualisation using the functions: *betweenness*, *assortativity*, *assortativity_degree* and *graph.data.frame*.

## Results

The nMDS analysis used to compare the resemblance between communities of each range showed a great differentiation between the native and the invaded ranges when taking into account all species (Fig. 2a) and alien species (Fig. 2b). The 15 sites within each range appeared grouped together without overlapping between ranges in both nMDS. Both ranges had a major dispersion, caused by the community differences amongst the surveyed sites.

The floristic composition differed slightly more amongst the sites in the invaded range (i.e. appeared more dispersed in the nMDS) than amongst those in the native one.

Regarding the co-occurrence results (Table 1), when all species were considered, in both ranges, the percentage of random associations is above 95%. If only alien species were considered, in the native and invaded range, the percentage of negative associations is 98.2 and 93.24, respectively. Meanwhile, the percentage of non-random associations within all species in the invaded range represents twice the value for that in the native range. If only alien species were analysed, this invaded value rises to 3.75 times the native value. When contrasting the type of associations, both ranges had more positive associations than negative: 54% of the non-random associations were positive in the native range, while in the invaded range, it is 53%. When only the alien species were compared, in the native range, 57% were positive associations compared to the 64% of the invaded range.

After the co-occurrence analysis, we applied the network analysis to those results to analyse the four networks (i.e. Spanish positive and negative associations networks and Chilean positive and negative associations networks). The resultant co-occurrence network plots for positive interactions (Fig. 3) showed that, in the native range, there is a large network formed by 62 species (a), a smaller network consisting of four species (b) and three isolated pairs (Fig. 3A). Meanwhile, in the invaded range, we observed a large network of 35 species (c), a medium-sized network of 12 species (d) and three isolated pairs (Fig. 3B). In both ranges, the larger networks seemed to be connected by alien species: *Moenchia erecta* (L.) P.Gaertn., B.Mey. & Scherb. in the native range (species 117 in Fig. 3A) and *Briza maxima* L. and *Tolpis barbata* (L.) Gaertn. in the invaded range (species 10 and 146, respectively in Fig. 3B).

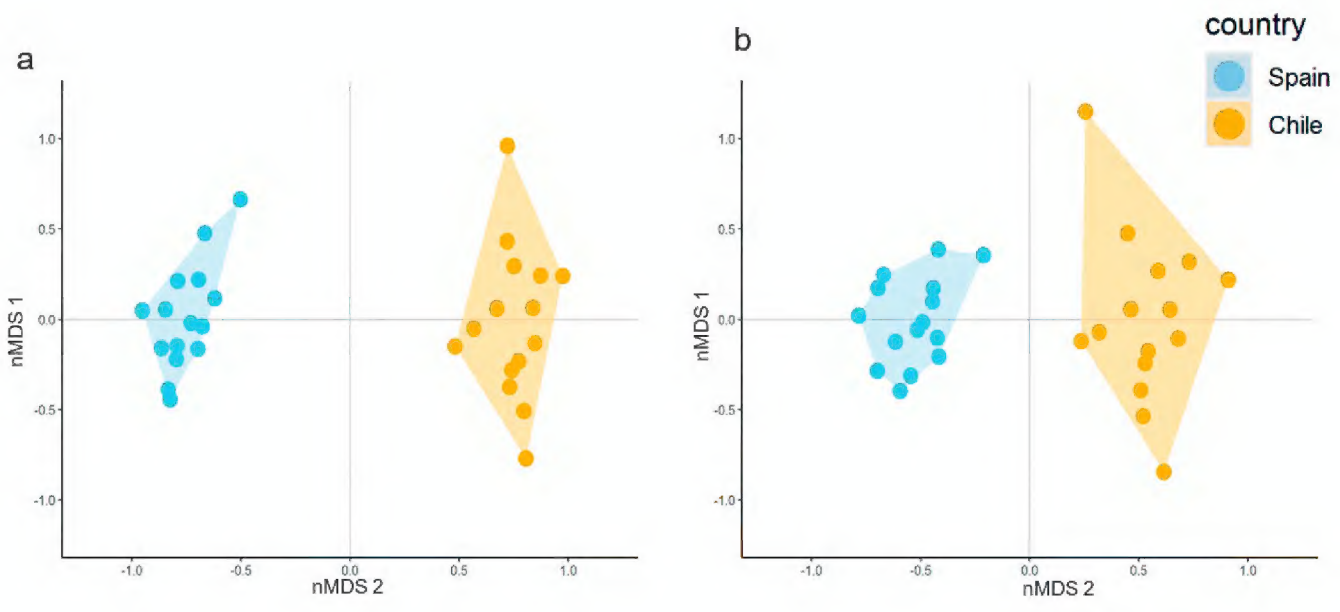


**Figure 2.** NMDS results for the sampling sites. Community resemblance between Spain (native range) and Chile (invaded range) was studied through non-metric Multidimensional Scaling (nMDS), based on the Bray-Curtis dissimilarity matrix with the abundance data. The graphic representation for the 30 sites surveyed considers: **a** all the species and **b** the pool of alien species. Sites in the native range are represented with blue dots, while sites in the invaded range are in orange. A polygon has been outlined connecting the sites of each country to improve the visualisation.

**Table 1.** Co-occurrence results for each range. Co-occurrence results of non-random associations for all species in Spain (native range), all species in Chile (invaded range), alien species in Spain and alien species in Chile.

| | | Non-random associations | | |
|---|---|---|---|---|
| **Country** | **Species group** | **%** | **positive** | **negative** |
| Spain | All | 2.29 | 102 (54%) | 85 (46%) |
| Chile | All | 4.84 | 90 (53%) | 80 (47%) |
| Spain | Alien | 1.80 | 31 (57%) | 23 (43%) |
| Chile | Alien | 6.76 | 57 (64%) | 32 (36%) |

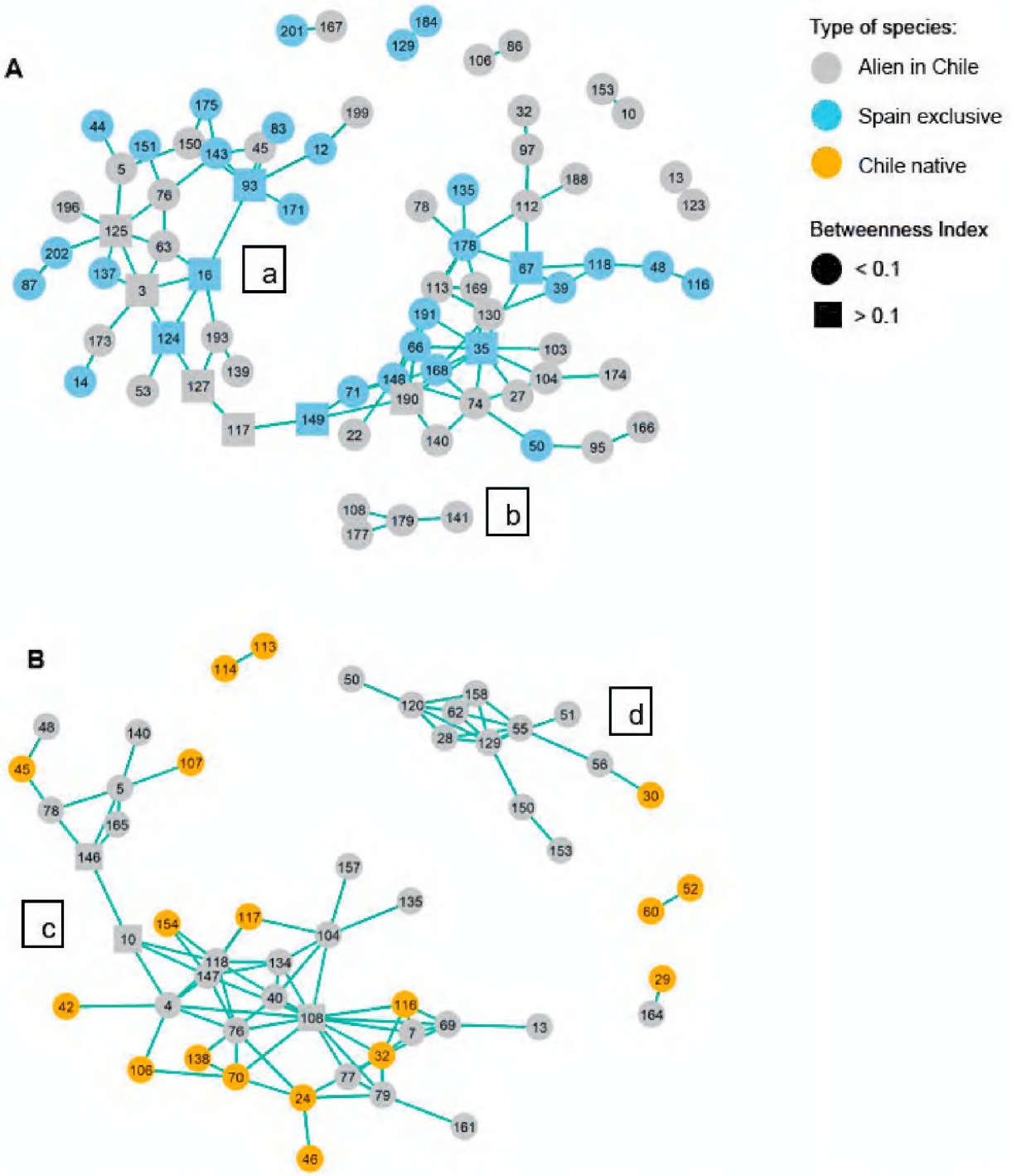


**Figure 3.** Visualisation of the co-occurrence network for both ranges. Green lines connect pairs of species that have a positive association. The numbers are the species ID and each of the three species types have a separate enumeration for each country (see Suppl. material 1: Table S1). To improve visualisation, only species involved in non-random positive associations are represented. **A** Positive association network of all species in the native range (Spain), where two networks have been identified, one large (a) and one small (b). **B** Positive association network of all species in the invaded range (Chile), where two networks have been identified, one large (c) and one medium (d).

Focusing on the type of species involved in each network, in the native range, both exclusive and alien species were homogeneously intermingled in the large network, whereas only alien species aggregated in the small network and in pairs. Both native and alien species were present in the invaded area within the large network. On the other hand, Chilean native species remained mostly in the outer zone of the network, except for *Carex bracteosa* Schwein., *Cicendia quadrangularis* (Lam.) Griseb., *Juncus pallescens* Wahlenb. and *Plantago firma* Kunze ex Walp. (species 24, 32, 70 and 116, respectively in Fig. 3B). In the same way, the medium-sized network was formed almost completely by alien species; only the Chilean native species *Cladanthus mixtus* (L.) Oberpr. & Vogt. (species 31 in Fig. 3B) was connected by one association. Regarding the three independent pairs, two of them were formed only by Chilean native species and one by one native and one alien species.

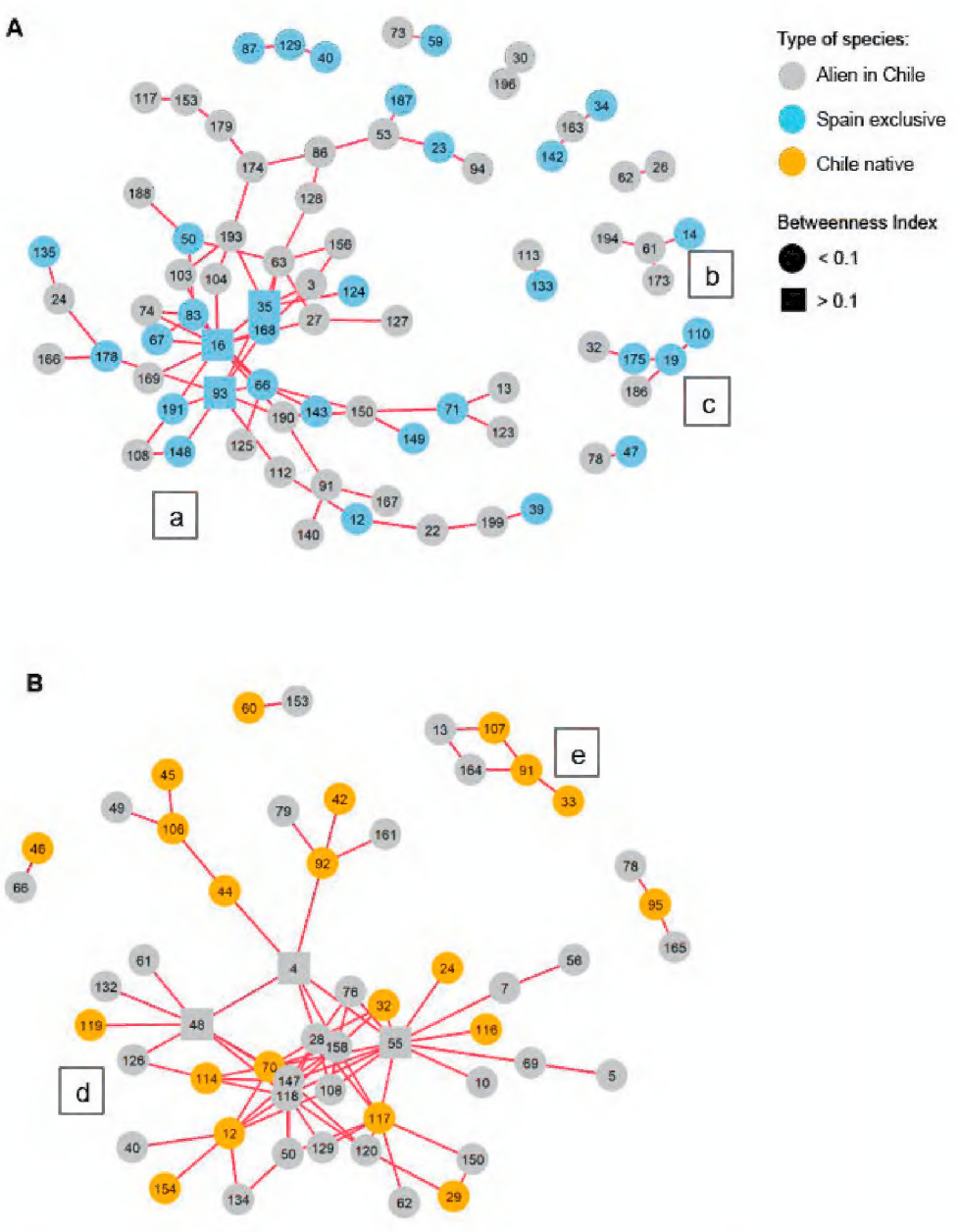


**Figure 4.** Visualisation of the co-occurrence network for both ranges.. Red lines connect pairs of species that have a negative association. The numbers are the species ID and each of the three types of species have a separate enumeration for each country (see Suppl. material 1: Table S1). To improve visualisation, only species involved in non-random negative associations are represented. **A** Negative association network of all species in the native range (Spain), where three networks have been identified, one large (a) and two smaller ones (b, c). **B** Negative association network of all species of the invaded range (Chile), where two networks have been identified, a large one (d) and a smaller one (e).

The co-occurrences network plots for negative associations (Fig. 4) revealed that, in the native range, there is a large network formed by 53 species (a), two smaller networks formed by 4 (b) and 5 (c) species, two trios and five isolated pairs (Fig. 4A). Meantime, in the invaded range (Fig. 4B), we observed a large network of 41 species (d), a smaller network of 5 species (e), one trio and two isolated pairs. Contrary to the network visualisation for positive associations, it was challenging to distinguish the species acting as main connectors in the larger negative networks. Focusing on the groups of species implied in each network, in both ranges, native and invaded, both alien and exclusive or Chilean native species intermingled evenly in the larger networks.

**Table 2.** Network analysis results for each range and type of association (positive and negative).

| Association sign | Range | Density | Assortativity coefficient | Assortativity degree |
|---|---|---|---|---|
| Positive | Native (Spain) | 0.04 | 0.06 | 0.06 |
| Positive | Invaded (Chile) | 0.07 | 0.21 | 0.10 |
| Negative | Native (Spain) | 0.03 | 0.01 | 0.11 |
| Negative | Invaded (Chile) | 0.06 | -0.10 | 0.02 |

**Table 3.** Species with a betweenness score greater than 0.10 for each of the four networks. Note that the 0.1 score is an arbitrary cut-off point.

| **Positive association network in the native range (Spain)** | | | | |
|---|---|---|---|---|
| ID | Species | Type | Betweenness score | Growth form |
| 149 | *Romulea bulbocodium* | Spain exclusive | 0.3347 | Geophyte |
| 117 | *Moenchia erecta* | Alien | 0.3330 | Terophyte |
| 127 | *Parentucellia latifolia* | Alien | 0.3315 | Terophyte |
| 190 | *Trifolium tomentosum* | Alien | 0.2633 | Terophyte |
| 35 | *Carlina racemosa* | Spain exclusive | 0.2513 | Terophyte |
| 124 | *Ornithopus perpusillus* | Spain exclusive | 0.2381 | Terophyte |
| 16 | *Aphanes microcarpa* | Spain exclusive | 0.1738 | Terophyte |
| 3 | *Agrostis castellana* | Alien | 0.1618 | Hemicryptophyte |
| 93 | *Jasione montana* | Spain exclusive | 0.1445 | Terophyte |
| 67 | *Euphorbia exigua* | Spain exclusive | 0.1410 | Terophyte |
| 125 | *Ornithopus pinnatus* | Alien | 0.1081 | Terophyte |
| **Positive association network in the invaded range (Chile)** | | | | |
| ID | Species | Type | Betweenness score | |
| 108 | *Petrorhagia prolifera* | Alien | 0.1950 | Terophyte |
| 10 | *Briza maxima* | Alien | 0.1568 | Terophyte |
| 146 | *Tolpis barbata* | Alien | 0.1436 | Terophyte |
| **Negative association network in the native range (Spain)** | | | | |
| ID | Species | Type | Betweenness score | |
| 93 | *Jasione montana* | Spain exclusive | 0.1904 | Terophyte |
| 16 | *Aphanes microcarpa* | Spain exclusive | 0.1467 | Terophyte |
| 35 | *Carlina racemosa* | Spain exclusive | 0.1170 | Terophyte |
| **Negative association network in the invaded range (Chile)** | | | | |
| ID | Species | Type | Betweenness score | |
| 55 | *Galium murale* | Alien | 0.2405 | Terophyte |
| 4 | *Anagallis arvensis* | Alien | 0.2170 | Terophyte |
| 48 | *Erodium botrys* | Alien | 0.11901 | Terophyte |

Focusing on the positive associations from the network analysis, the invaded range had superior values in the three calculated parameters (density, assortativity coefficient and assortativity degree), the assortativity coefficient values (3.5 times higher in the invaded range) being outstanding. Regarding the negative associations from the network analysis, the invaded range had a density value double that for the native range; however, the assortativity degree was 5.5 times lower. The assortativity coefficient of the invaded range stood out as the only negative value within the networks, indicating that nodes tend to connect with nodes of different type (Table 2). This means that the alien species tend to form negative associations with native species and vice versa.

To obtain information on the importance of species in the community structure, the betweenness score was calculated. When observing the positive association network, in the native range, there are several species with betweenness values higher than 0.1, five of them are alien species and six are exclusive to Spain. In the invaded range, there are only three species, all of them alien. When looking at the negative association network, only three species are above 0.1 in both ranges. In the native range, these species are all exclusive to Spain, while in the invaded range, there are, once again, alien species.

## Discussion

Community assembly of Mediterranean herbaceous species differs between Spain and Chile with little resemblance amongst community structures in the native and invaded ranges. Regarding community structure in the invaded range, most of the species that establish non-random associations correspond to alien species, which surprisingly act as keystones within the community. In the invaded range, the assembled community has higher network connectivity. Moreover, alien species in the invaded area tend to assemble more amongst them displacing native species to the edges of the network.

Although there were more alien than native species in the invaded study area (Martín-Forés et al. 2012), both ranges showed a contrasting resemblance, differing in their community structure when the abundance of all species was taken into account (Fig. 2a). This pattern persisted when comparing alien species common to both countries, suggesting that alien species are particularly significant in shaping communities in the invaded range (Fig. 2b). After the introduction related to the Spanish colonisation in the 16$^{th}$ century (Martín-Forés et al. 2015), climate, amongst other abiotic conditions, strongly influenced the establishment of alien species in the invaded range, as it also does on the community assembly in the native range (Figueroa et al. 2004; de Miguel et al. 2016; Rota et al. 2017). Despite the climatic similarity, the higher water deficit in the invaded area (up to 8 months in the Mediterranean Region of Central Chile versus 4 months in Spain; Martín-Forés et al. (2015)) and the local differences in livestock management between both ranges (del Pozo et al. 2006; Casado et al. 2015), may be influencing the heterogeneity found within the two countries. Differences between Chilean communities at the regional scale may be due to the regional precipitation gradient that conditions water availability (Martín-Forés et al. 2015) (Fig. 2).

Our results showed that the associations of the alien species differed within the plant communities in both native and the invaded ranges. This suggests that the associations of alien species in the invaded area is an inherent property of being away from their native range, rather than a property of the species itself (Stotz et al. 2020). For example, alien species can tend to aggregate amongst them in the invaded range and they have been found to establish preferably in species-poor places with greater levels of disturbance and higher nutrient availability, biomass and competition (Stotz et al. 2020). We found that, in both ranges, less than half of the total number of species are involved in non-random associations. The non-random pattern of species assemblage displayed by the communities in both ranges (i.e. the higher or lower ratio of co-occurrence than that expected from random; Griffith et al. 2016), suggested that these communities are structured by deterministic processes instead of stochastic ones (Krasnov et al. 2010). It seems that the co-existence of species for longer periods of time tended to randomise the associations, as in Spain, the percentage of non-random association was smaller than in Chile. This is in slight contrast to the results obtained by de Miguel et al. (2016), in which they detected that, in Chile, the spatial segregation of species was similar to Spain. This demonstrates that a longer co-existence time does not determine a greater spatial segregation of species. Conventional knowledge indicates that species interactions, especially competition, are the main forces shaping community structure, but habitat heterogeneity is also a source of non-random spatial distributions of species (Ulrich 2004; Kraft et al. 2015). Even though both areas harbour similar climatic conditions, other regional factors, such as water availability (Acosta et al. 2008), soil fertility (Holmgren et al. 2000; Price et al. 2014) and fire regimen (Brotons et al. 2013) under the combined effect of grazing, could affect this association processes revealing a divergence in the communities (Martín-Forés et al. 2012; Peco et al. 2017).

The network analysis applied to the co-occurrence patterns resulted in a visual output that revealed meaningful structural information (Newman 2003; Fortunato 2010). At the community level, communities in both the native and invaded ranges have very poorly connected co-occurrence networks, both positively and negatively, as evidenced by the near-zero density (Newman 2003). This supports the idea that. in both ranges, grassland communities are primarily driven by abiotic factors rather than by biotic relationships between species, whether native or alien (Casado et al. 2015; Martín-Forés et al. 2015). The assortativity degree results manifested similar tendencies in both countries, where species slightly tend to connect to other well-connected species (Fig. 3). This is coherent with the typical properties of biological networks, where it is common to find large clusters of nodes with a high level of internal connections, but weakly connected to other clusters, known as the modularity of a network (Sah et al. 2014). This modularity in biological networks is known to promote cohesion and contain disturbances, as species in one module are more tightly linked to each other than to species in other modules (Olesen et al. 2007; Stouffer and Bascompte 2011). This structure perhaps is an additional strategy of the Mediterranean grasslands that allows them to be particularly resilient systems despite the constant disturbances that characterise the Mediterranean Region, such as fire, thermal oscillation, irregular

rainfall distributions between years and the summer drought (Henkin et al. 2010; Acosta and Pineda 2012).

Observing the network structure, in the native range, alien species integrate with the rest of the species in a large network, as the "alien" grouping in the native range is an artificial group that allows the comparison with the invaded range (see Figure 3A). In the invaded range, some alien species appear to be connected to each other and native species only participate partially in these networks, without constructing independent networks of their own. The fact that the percentage of associations between alien species was almost four times higher in the invaded range than in native range (Table 1) indicates that, in the invaded area (Chile), the alien species tend to be more connected. This result could be due to shared habitat preferences amongst alien species, as found out by the study conducted in grasslands by Stotz et al. (2020). Furthermore, in the invaded range, amongst alien species, positive associations were higher and negative associations lower than in the area of origin, similar to the findings of Braga et al. (2018) in a large-scale study. This suggests that facilitation mechanisms are occurring between alien species in the invaded range, which could, in turn, lead to an "invasional meltdown", where a successful invader may trigger subsequent invasions, increasing their chance of survival and ecological impact (Simberloff and Von Holle 1999; but see Divíšek et al. 2018).

Preferences for associations that occur between species also vary between ranges and the results of the invaded area are striking. Only a group of species from the area of origin (Spain) has been able to remain in the invaded area (Chile) and naturalise (Martín-Forés et al. 2012), probably due to having similar naturalisation mechanisms. Once established, the alien species tend to positively associate amongst them and negatively with the native species, with the exemption of few native species that positively associate with the alien ones (Figs. 3b and 4b and Table 2). This could be due to facilitation mechanisms between alien species (Braga et al. 2018); similarly, the tolerance of plants to grazing pressure could be influencing their configuration (del Pozo et al. 2006).

The results of the network analysis are striking because when literature from other Mediterranean areas with the same source-invader relationship has compared the assemblage in terms of abundance, alien species assemble similarly in their source and recipient communities (Firn et al. 2011; Parker et al. 2013; Colautti et al. 2014; Pearson et al. 2018). In contrast, by applying this methodological approach, we can observe that alien species assemble very differently in the invaded area. It seems that the set of species that arrive in the invaded area of distribution reorganise themselves differently from the original community of which they formed part in the native area (Spain), coexisting with native species with which they show less affinity.

Concerning the species acting as keystones, alien species in the invaded range have an important role in the community structure. We expected Chilean native species would play a key role in Chilean communities, but our results suggest the opposite. In the invaded range, alien species showed the highest betweenness score, acting as a cornerstone for both positive and negative associations. In Chilean agroecosystems, eradication of alien species has not been a main management strategy (Root-Bernstein

and Jaksic 2013), which could be the explanation for alien species developing key roles within the community. The implications for management strategies and conservation practices are, therefore, delicate. On the one hand, after a disturbance, alien species could preserve the rest of the community in a well-connected manner (but see Carmona et al. 2017), enhancing the resilience and functional persistence of ecosystems by strengthening the network interacting with native species (Aslan 2019). On the other hand, if left unmanaged, those alien species could displace the Chilean native flora. In addition, since the introduction and naturalisation of these key alien species are associated with grazing (Arroyo et al. 2000; Figueroa et al. 2004; Martín-Forés et al. 2012) and that the long-term stability of these grasslands depends on certain intensity and periodicity of human activities (del Pozo et al. 2006), any land-use changes could trigger their spread or regression. Further studies on elucidating this trend would be desirable.

Meanwhile, the alien species that play important roles in the invaded range do not do so in the native range. In the native range, a greater number of species were actively involved in shaping the network (i.e. displayed high betweenness), providing greater stability against disturbances, probably because these Spanish agro-ecosystems have been maintained over millennia (Acosta and Pineda 2012; Landi et al. 2018).

Although it is questionable whether theoretical models can accurately predict assembly patterns and how environmental factors and land uses might alter the effects of species interactions on species co-occurrence (Ulrich et al. 2017), unseen patterns have emerged. The next step may be to explore the networks in detail to understand spatio-temporal dynamics on a regional or patch scale and identify patterns that may depend on the scale of analysis (Smith et al. 2013; Escobedo et al. 2021). However, we considered processes at a small spatial scale (0.5 $m^2$), because, in grasslands, at larger spatial scales, more positive correlations between native and alien species can be found, but they are driven by environmental heterogeneity instead of by biotic interactions, giving rise to misleading results (Davies et al. 2005). In addition, functional traits are known to play a key role in community assembly and invasiveness (Tecco et al. 2010; de Bello et al. 2012; HilleRisLambers et al. 2012; Thuiller et al. 2012; Colautti et al. 2014; Galán Díaz et al. 2021) and positive associations between rare species persist across taxon assemblages (Calatayud et al. 2020). Similarly, certain growth forms can be displaced by alien species in grassland communities (Guerin et al. 2019), therefore including species' trait syndromes in further studies of species co-occurrence would help unravelling insights of the assembly process. It should also be noted that our results may be conditioned by the short time period included in the analysis (one year) as the Mediterranean climate region suffers from a large inter-annual variation in plant community composition. This variation is due to the irregularity of the rainfall regime that encourage alternatively the abundance of more or less drought-tolerant species (Acosta et al. 2008; Peco et al. 2009; Rota et al. 2017). We recommend further studies to explore changes in community structure over time via resampling the same community after a certain period of time (in this case, the changes are more perceptible after 4–6 years according to Martín-Forés et al. 2016) and applying the methodology

described here. This will allow accounting for failure of establishment and invasion lag periods in the process of community assembly.

Our novel methodology, proposed in this paper, improves our understanding of how the naturalisation process affects community assembly and structure. Network analyses are a free, easy-to-implement and straightforward visual tool that can be widely used in community ecology, to unravel assembly patterns, which would enable the prediction of changes in ecosystem structure and functioning under different changing scenarios. Similarly, in studies of invasion ecology, it allows revealing shifts in native communities and elucidates the role of multiple invaders into communities.

Thus, the identification of negative and positive associations, as well as elucidating which species act as keystones, is presented as a step forward in invasion ecology studies and as a tool to help designing restoration and conservation strategies in socioecological systems (Root-Bernstein and Jaksic 2013). This is particularly relevant in areas where multiple environmental and social factors operate and intermingle, such as in the Mediterranean biome (Doblas-Miranda et al. 2017). Grazing systems in Mediterranean Regions are essential as sustainable and biodiversity-friendly food production systems of the future, amongst other ecosystem services, such as hydrological regulation and carbon sequestration (Acosta and Pineda 2012; Root-Bernstein et al. 2017), being absolutely critical in the actual context of global change (Van Kleunen et al. 2015; Cramer et al. 2018; IPCC 2018; Lionello and Scarascia 2018).

## Conclusion

With this work, we have proved the utility of combining network analysis to co-occurrence analysis, as it has permitted the process of exploring complex sets of data and results in a very interesting way. Our results showed that the community assembly pattern differs between the native and the invaded ranges. Alien species that became naturalised in the invaded area re-assembled differently, tending to co-occur more amongst them and to avoid interaction with native species. Moreover, alien species acted like keystones in the communities of the invaded range. The key role displayed by alien species in Chilean communities could cause an invasional meltdown and threaten the native biodiversity. Conservation and managing strategies should focus on monitoring and controlling their potential spread and developing early detection strategies especially for the alien species identified as keystones.

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## Supplementary material 1

**Table S1. Species ID for each country and type of species**

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Data type: species data

Explanation note: Species ID for each country, type of species and relative abundance. Note that each species has a different ID in each range.

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